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Aspidoscelis costatus costatus (Squamata, Teiidae): high elevation clutch production for a population of whiptail lizards

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Abstract

Clutch size and number of clutches per reproductive cycle are important life history traits that can be influenced by anatomical, physiological, evolutionary, and ecological factors. This report on the clutch size and number of clutches of an endemic Mexican whiptail lizard, *Aspidoscelis costatus costatus* (Cope, 1878), is based on a study of population at an unusually high elevation for a member of this genus. The study site is located in Ixtapan de la Sal, southeastern Estado de México, Central Mexico, at 2090 m a.s.l. Lizards were sampled in June 2006, and from May to July 2007, where females of *Aspidoscelis costatus costatus* were collected by hand along a drift fence. Female reproductive condition was evaluated based on abdominal palpation for presence of developing eggs; clutch size was determined by actual counts of either vitellogenic follicles or oviductal eggs. The smallest reproductive female was 77 mm snout-vent length; females produced a minimum of two clutches during the breeding season, the mean clutch size of 6.5 eggs (n = 33) was one of the largest reported for the genus. However, both length and width of its eggs, and the relative clutch mass have not been diminished by development of a large clutch. Additionally, comparisons of clutch size were undertaken within the polytypic *A. costatus* complex, within the genus *Aspidoscelis*, and between certain genera of whiptail lizards. This apparently represents the first study of whiptail lizards (genus *Aspidoscelis*), assessing the aforementioned reproductive characteristics, in a population above 2000 m.

Key Words

Balsas Basin Whiptail, Central Mexico, clutch size, female size, Estado de México, relative clutch mass

Introduction

Knowledge of the reproductive potential of a population is fundamental to understanding its life history (Stearns 1989) and ecological status. Thus, determination of clutch size and number of clutches per activity cycle are the primary steps in assessing reproductive output. Several factors may act as potential sources of variation in clutch size including ecological (Horváthová et al. 2013), evolutionary (Suárez-Rodríguez et al. 2018; Taylor et al. 2006), anatomical (Suárez-Varón et al. 2019; Taylor et al. 2006), and physiological factors (Méndez-de la Cruz et al. 1993). In general, *Aspidoscelis* lizards are considered to be wide foragers in search of their prey (Paulissen 1987; Utsumi et al. 2020). Due to their active foraging strategy, body shape, and escape strategies, species in the genus *Aspidoscelis*

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tend to show a relatively small clutch size, proportional to their body mass (Vitt and Breitenbach 1993). Previous studies have shown that both clutch size and number of clutches per cycle may vary in a species based on latitude or elevation (McCoy and Hoddenbach 1966; Dixon et al. 1971; Taylor et al. 1992); however, this does not apply to all Squamata species (Fitch 1985; Meiri et al. 2013).

Although Western Mexican Whiptail [*Aspidoscelis costatus* (Cope, 1878)] is currently treated as a polytypic species (Reeder et al. 2002) with eight subspecies, it is generally understood that it is actually a non-monophyletic species complex of several species including *Aspidoscelis costatus costatus* (Cope, 1878) = Balsas Basin Whiptail [Reeder et al. 2002 (diversity in the genus); Tucker et al. 2016 (nomenclature based on proof of masculine rather than feminine gender of the generic name); Barley et al. 2019 (diversity in the *sexlineatus* species group in México)]. Based on Tucker et al. (2016) the name *A. costatus costatus* replaces *A. costata costata* (sensu Reeder et al. 2002). This species inhabits various ecological habitats and elevations in the states of Mexico, Guerrero, Morelos, Puebla, Tlaxcala, and Oaxaca (Maslin and Secoy 1986; Gómez-Benitez et al. 2016; Méndez de la Cruz et al. 2018; Barley et al. 2019). Despite the ecological and evolutionary constraints (i. e., body shape, SVL, foraging mode, predator escape tactics) on clutch size within the genus *Aspidoscelis* (Vitt and Price 1982; Taylor et al. 2006), and although several congeners grow to a much larger SVL [i. e., *Aspidoscelis stictogrammus* (Burger, 1950), *Aspidoscelis sacki* (Wiegmann, 1834) and *Aspidoscelis costatus occidentalis* (Gadow, 1906)], *A. costatus costatus* shows the largest clutch size reported to date (7.7 eggs, range 4–14; López-Moreno et al. 2016). Our study reports the clutch size and number of clutches in a different unique high-elevation population (> 2000 m) of Balsas Basin Whiptail (Fig. 1), which is also among the largest clutch sizes in a population of the genus *Aspidoscelis*.

Methods

The study site is located at Ixtapan de la Sal, southeastern Estado de México, north of the Río Balsas Basin, in Central Mexico (18°50'30"N, 99°39'0"W), at an altitude of 2090 m a.s.l. (Fig. 2), which is considered an unusually high elevation for teiid lizards (Vitt and Breitenbach 1993). Vegetation at the locality consisted of coniferous forest interspersed with tropical deciduous forest and grassland (Fig. 3). The climate is semi-humid and semi-warm with summer rains which typically occur from mid-June through mid-September with annual variation (Hernández-Gallegos and Domínguez-Vega 2012).

Females of *A. costatus costatus* were captured by hand along a drift fence during their activity period (09:00–17:00 h) in June 2006, and from May to July 2007. The reproductive condition of each adult female was evaluated based on an abdominal palpation and a visual assessment, where the vitellogenic/gravid females showed an expanded contour in the abdomen region (Suárez-Varón et al. 2019). Snout-vent length (SVL) and mass were recorded to the nearest 1 mm and 0.1 g, respectively. Only vitellogenic and gravid females were euthanized via an intraperitoneal injection of sodium pentobarbital, and ovaries and oviducts were removed and placed in 10% neutral buffered formalin. Clutch size was estimated by counting vitellogenic follicles (≥ 3 mm, precision 0.01 mm, López-Moreno et al. 2016) or shelled oviductal eggs when present. We also calculated the relative clutch mass (RCM, based

Figure 1. Adult female of Balsas Basin Whiptail, *Aspidoscelis costatus costatus*, from Ixtapan de la Sal, Estado de México, México.

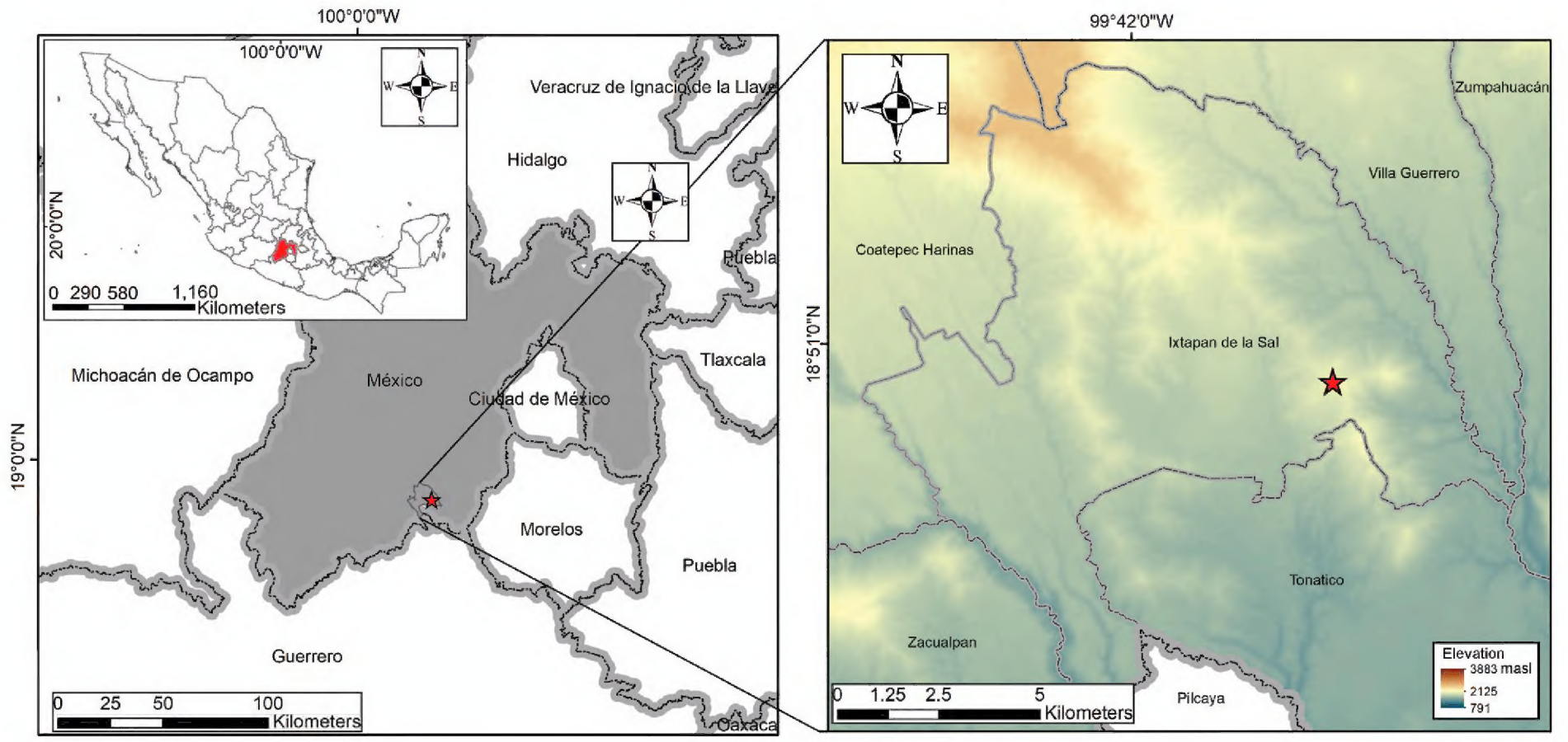

Figure 2. Map showing the study site where Balsas Basin Whiptail, *Aspidoscelis costatus costatus*, was collected at Ixtapan de la Sal, Estado de México, México.

Figure 3. Habitat of Balsas Basin Whiptail, *Aspidoscelis costatus costatus*, at Ixtapan de la Sal, Estado de México, México.

only on oviductal eggs) by dividing clutch mass (precision 0.0001 g) by female's total mass (including clutch weight; Tinkle 1972). All measurements were carried out following appropriate guidelines for Scientific Animal Use, unnecessary stress was avoided, and individuals were humanely sacrificed. Females were deposited in the Laboratorio de Herpetología, Facultad de Ciencias, Universidad Autónoma del Estado de México, México (voucher numbers pending). All lizards were collected under the Scientific Collector Permit, FAUT 0186 SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales).

We evaluated the differences between slopes and intercepts of regression lines of vitellogenic follicles and number of oviductal eggs against SVL. The relationship of clutch size and SVL of females was evaluated by Pearson's correlation coefficient. Moreover, we evaluated the differences (using a Student's *t* test) of clutch size, size of eggs and RCM of *A. costatus costatus* with other species of *Aspidoscelis* using data from literature. All data were tested for normality via a Kolmogorov-Smirnov test. Analyses were performed in STATGRAPHICS Centurion XV.II, and results were deemed significant if $p < 0.05$.

Results

The smallest reproductive female was 77 mm SVL, a larger size at first clutch production than recorded for several subspecies of *A. costatus* (Walker et al. 2003; Walker 2008a, b, 2010). Females of *A. costatus costatus* produce at least two clutches during the breeding season as some females (44.4%) with oviductal eggs also possessed vitellogenic ovarian follicles. All variables were normally distributed (since the fit tests show $p > 0.05$). We estimated clutch size by number of vitellogenic follicles (mean = 6.3 ± 1.7, range 4–10, n = 24) and oviductal eggs (mean = 7.0 ± 2.1, range 4–10, n = 9) together, because the slopes ($b = 0.160 \pm 0.022$, $b = 0.189 \pm 0.091$, respectively) and intercepts ($a = -8.054 \pm 2.023$, $a = -11.009 \pm 8.746$, respectively) of regression against SVL did not differ significantly ($p = 0.6799$, $p = 0.6212$, respectively). The mean mass of females *A. costatus costatus* (including both vitellogenic and gravid) was 21.4 ± 1.1 g (median 21.2, range 10–35, n = 33). The mean SVL was 91.2 ± 1.5 mm (median 92 mm, range 77–111, n = 33) and the mean clutch size was 6.5 ± 1.8 eggs (median 6 eggs, range 4–10, n = 33), and both traits were positively correlated (Pearson's correlation, $R^2 = 0.7725$, $p < 0.0001$, Fig. 4). The clutch size of *A. costatus costatus* is larger than the mean clutch size in the genus *Aspidoscelis* (ca. 3.2 eggs, $t_{67} = 9.46$, $p < 0.0001$; see Meiri 2018 for the clutch size in the genus). The mean RCM

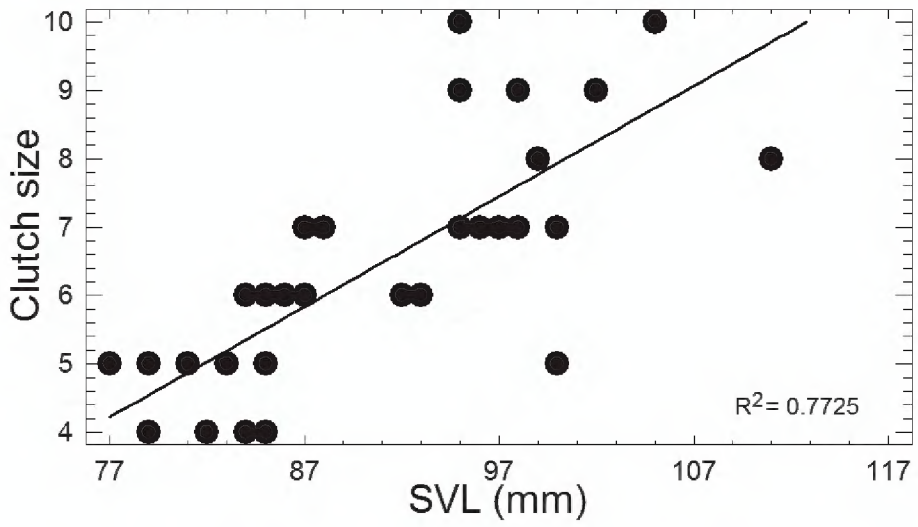

Figure 4. Relationship between clutch size and snout-vent length (SVL) in Balsas Basin Whiptail, *Aspidoscelis costatus costatus*, from Ixtapan de la Sal, Estado de México, México.

was 0.17 ± 0.02 (range 0.14–0.19, n = 9), and did not differ (t_{18} = -0.71, p = 0.4868) from RCM in the genus *Aspidoscelis* (0.18; see Mesquita et al. 2016 for the RCM in the genus). The shelled oviductal eggs had a mean width of 8.5 ± 0.88 mm (range 6.8–9.9, n = 63), mean length of 14.1 ± 1.8 mm (range 10.9–17.2, n = 63), and mean mass of 0.62 ± 0.14 g (range 0.39–0.78, n = 51). Both mean width (8.4 mm) and mean length (14.8 mm) of eggs in the genus *Aspidoscelis* (Table 1) are not significantly different from *A. costatus costatus* (t_{77} = -0.51, p = 0.6126, t_{77} = 1.81, p = 0.0744, respectively).

Discussion

Aspidoscelis is the most speciose genus (43 species; Uetz and Hõsek 2020) within the family Teiidae. This genus is divided into five clades (Reeder et al. 2002) and shows a low diversity (Vitt and Breitenbach 1993) and general absence from high elevations (> 2000 m; Vitt and Pianka 2004). However, two species in Central Mexico also occur at unusually high elevations: *Aspidoscelis gularis* (Baird & Girard, 1852), up to 2358 m a.s.l. at Sierra de Santa Catarina, México, D. F. (Hernández-Gallegos et al. 2009), and *A. costatus costatus*, up to 2750 m a.s.l. at La Malinche National Park, Tlaxcala (Méndez de la Cruz et al. 2018). To our knowledge, our study represents the first record, within the genus *Aspidoscelis*, including detailed reproductive traits (i. e., clutch size and clutches per cycle) from above 2000 m.

There have been numerous studies of reproductive characteristics in populations currently allocated to *A. costatus*. Larger clutch means and maximum clutch sizes characterize the two samples of *A. costatus costatus* from the southerly latitudes and higher elevations in Estado de Mexico (this study, Lopez-Moreno et al. 2016), compared to smaller clutch means and smaller maximum clutch sizes for samples of *Aspidoscelis costatus barrancarum* (Zweifel, 1959) (mean 3.92, range 2–7 eggs, SVL 70–107 mm), *Aspidoscelis costatus huico* (Zweifel, 1959) (4.4 ± 0.23, 2–8 eggs, SVL 65–105 mm), *Aspidoscelis costatus nigrigularis* (Zweifel, 1959) (4.4 ± 0.26, 1–7 eggs, SVL 62–105 mm), and *Aspidoscelis costatus gris-*

Table 1. Mean egg length and mean egg width for selected parthenogenetic* and gonochoristic species in the genus *Aspidoscelis*.

Species	Egg length (mm)	Egg width (mm)	Source
Aspidoscelis costatus barrancarum	14.0	9.0	Walker et al. 2003
Aspidoscelis costatus costatus	**14.1**	**8.5**	**This study**
Aspidoscelis costatus costatus	14.7	8.8	López-Moreno et al. 2016
Aspidoscelis costatus huico	14.4	8.2	Walker 2008a
Aspidoscelis costatus nigrigularis	14.5	8.0	Walker 2008b
*Aspidoscelis cozumela**	15.3	8.5	Manríquez-Morán et al. 2005
Aspidoscelis gularis	13.5	7.2	Vitt and Breitenbach 1993
Aspidoscelis hyperythrus	14.5	7.4	Vitt and Breitenbach 1993
Aspidoscelis inornatus	13.5	6.7	Vitt and Breitenbach 1993
Aspidoscelis lineatissimus	14.4	9.7	Ramírez-Bautista et al. 2000
*Aspidoscelis neomexicanus**	15.9	7.9	Vitt and Breitenbach 1993
Aspidoscelis parvisocius	13.5	8.5	Vitt and Breitenbach 1993
Aspidoscelis sacki	16.4	10.1	Vitt and Breitenbach 1993
*Aspidoscelis sonorae**	14.2	8.2	Vitt and Breitenbach 1993
*Aspidoscelis tesselatus**	17.1	9.3	Vitt and Breitenbach 1993
Aspidoscelis tigris	17.9	10.0	Vitt and Breitenbach 1993
*Aspidoscelis uniparens**	13.1	7.1	Vitt and Breitenbach 1993

eocephalus (Zweifel, 1959) (3.8 ± 0.37, 2–6 eggs, SVL 61–96 mm) from more northerly latitudes and lower elevations (Walker et al. 2003; Walker 2008a, b, 2010). However, egg sizes for these forms do not differ significantly (Table 1). Clutch sizes are larger in cold regions (Meiri et al. 2013), however, whether these clutch differences are reflective of different ecologies or indicators of species divergence is a pending question. It is well to remember that populations presently treated as *A. costatus* may include two or more closely related species (Reeder et al. 2002; Barley et al. 2019), though no instances of syntopy between these putative species are believed to occur.

Both ecological and evolutionary factors may adjust the reproductive output in lizards (Suárez-Rodríguez et al. 2018; Suárez-Varón et al. 2019). In general, lizards have clutch sizes that vary with the female´s size, foraging mode or predator escape tactics (Vitt and Price 1982). In species of the genus *Aspidoscelis*, small clutch size is a general tendency (Dunham and Miles 1985; Vitt and Breitenbach 1993; Hernández-Gallegos 2004; Meiri 2018). However, the mean of 6.5 eggs found in *A. costatus costatus*: (1) is larger than the mean clutch size in the genus *Aspidoscelis*, and (2) represents one of the largest clutch sizes reported for this genus (including both gonochoristic and parthenogenetic lineages; Meiri 2018). It is noteworthy that females of *A. costatus costatus* have a similar mean clutch size (6.5) and a smaller mean SVL (91.2 mm) compared with the southern Mexican congener *A. communis* (Cope, 1878) (mean clutch size 6.6 eggs, mean SVL 96.5, Walker 1982), and a larger clutch size than the largest females in the genus, *A. sacki* (mean clutch size 5.9 eggs, mean SVL 112 mm, Walker 1981; Hernández-Gallegos et al. 2011). Furthermore, similar to the site of Tonatico (López-Moreno et al. 2016), based on a linear model (assuming absence of phylogenetic effects), females from Ixtapan de la Sal with an average of 91.2 mm SVL are predicted to have a clutch size of only 4.8 eggs (Hernández-Gallegos 2004) rather than 6.5

eggs. However, the clutch size of *A. costatus costatus* at Ixtapan de la Sal is smaller than that of *A. costatus costatus* from Tonatico, Estado de México (1500–1600 m a.s.l; López-Moreno et al. 2016). Interestingly, the predicted clutch size for Estado de México aligns with clutch sizes reported for of *A. costatus barrancarum*, *A. costatus huico*, *A. costatus nigrigularis*, and *A. costatus griseocephalus* (see Walker et al. 2003; Walker 2008a, b, 2010). An additional difference between populations is the number of clutches per cycle, multiple in Ixtapan de la Sal (as in *A. costatus barrancarum*, Walker et al. 2003) against a single clutch per reproductive season in Tonatico (López-Moreno et al. 2016). As in other lizards including *Aspidoscelis* and *Sceloporus* (McCoy and Hoddenbach 1966; Dixon et al. 1971; Taylor et al. 1992; Lemos-Espinal et al. 1998; Ramírez-Bautista et al. 2011), this intraspecific variation in clutch size and number of clutches, could be explained for the difference in elevation, rainfall, temperature, and vegetation (Muñoz-Manzano 2010; López-Moreno et al. 2016), although this is not true for all species or populations (Fitch 1985; Meiri et al. 2013).

The elongated body shape (typical of *Aspidoscelis* lizards) is one constraint on clutch size in the genus, but there may also be an added phylogenetic constraint in certain species (see Taylor et al. 2006; Barley et al. 2019). However, also to be considered are the costs associated with carrying a large clutch in active foragers. This could restrain clutch size in a gravid female of *Aspidoscelis* through natural selection, since the ability of a lizard to carry "extra" mass would directly affect both the probability of escape from a predator (Vitt and Congdon 1978; Huey and Pianka 1981) and success in foraging. In this sense, as previously recorded in *A. costatus costatus* from Tonatico (López-Moreno et al. 2016), an increase of clutch size in *A. costatus costatus* at Ixtapan de la Sal, has not affected the size of its eggs (Table 1), or its RCM which did not differ from the RCM average within the genus *Aspidoscelis* (Mesquita et al. 2016) and is near to *A. costatus costatus* from Tonatico (0.19; López-Moreno et al. 2016).

The anatomical appellation "whiptail lizards" not only refers to individuals of the genus *Aspidoscelis*, distributed in North and Central America, but also to lizards of the teiid genera *Ameivula*, *Aurivela*, *Cnemidophorus*, *Contomastix*, and *Glaucomastix* (Goicoechea et al. 2016); *Cnemidophorus* is distributed in Central and South America and the other four genera are restricted to South America. Although details of reproduction differ among whiptail species of these genera, the variation is within the evolutionary and ecological limits provided by oviparity (i. e., all species), lack of parental care (i. e., all species), and clutch frequencies controlled by seasonality (i. e., *A. costatus costatus*, this study) or not (i. e., *Cnemidophorus murinus* = *C. ruthveni*, Burt, 1935; Dearing and Shall 1994) as related to latitude and/or altitude. Variation in clutch sizes is both dependent (i. e., *A. costatus costatus*) and independent of body size (i. e, *C. murinus* = *C. ruthveni*, Dearing and Schall 1994). The species of this study, *A. costatus costatus* from Ixtapan de la Sal, Estado de México, México, is an example of a whiptail representative of its genus which occurs in the subtropics at a highest known altitude for a reproductive study in the genus. Its reproductive cycle is expressed within seasonal constraints, females are of moderately large reproductive size of 77–111 mm SVL, they produce a relatively large mean clutch of 6.5 ± 1.8 eggs which is correlated with SVL. Compared with a whiptail species of another teiid genus in a coastal area of the state of Ceará, Brazil, namely *Ameivula ocellifera* (Spix, 1825) (Harvey et al. 2012), Zanchi-Silva et al. (2014) found that adult females produce multiple clutches extending throughout the year, but peaking at the end of the rainy season, has a mean clutch size of only 1.98 ± 0.56 eggs that is positively associated with female body size. However, Sales and Ferire (2016) reported no correlation between clutch size and SVL in *A. ocellifera*, a difference that requires clarification as to whether it represents accidents of sampling, geographic variation, or a taxonomic causation.

Described as having peculiar reproduction, the whiptail lizard of Bonaire Island, Netherland Antilles, South America, was referenced as *C. murinus* by Dearing and Schall (1994). It is here considered to be the most divergent example of reproduction compared with a form such as *A. costatus costatus*. However, Ugueto and Harvey (2010) elevated this insular population to species status using an extant subspecific name, with newly recognized *C. ruthveni* now considered to be restricted to Bonaire and Klein Bonaire islands and *Cnemidophorus murinus* (Laurenti, 1768) being restricted to Curaçao and Klein Curaçao islands. Unlike most whiptail lizard species which mainly consume arthropods, as is true of *A. costatus costatus* (Muñoz-Manzano 2010), both *C. ruthveni* and *C. murinus* are not only herbivorous, they exist in very dense populations on their respective islands. Dearing and Schall (1994) reported that females of the Bonaire Island whiptail species (maximum SVL of 116 mm), *C. ruthveni* sensu Ugueto and Harvey (2010), "…typically [produce a clutch of] one very large egg, but some females may produce two eggs." Also, that some insular lizards may produce smaller clutches which produce larger hatchlings (than closely related mainland species of similar size) is a very well-known phenomenon called the island syndrome (Novosolov et al. 2013).

Although data collected suggest a high reproductive output in *A. costatus costatus* at Ixtapan de la Sal, there are multiple variables that should still be investigated such as dorsal coloration, interlimb distance, and coelomic volume. These future studies will provide a holistic view of reproduction to see if the females in our population have adopted atypical strategies (i. e., seasonal dorsal coloration and widening of the abdominal area), which help to maintain a high-reproductive output as in *A. costatus costatus* from Tonatico (López-Moreno et al. 2016). Finally, further studies on other populations are needed to clarify the idea that probably a large clutch size is characteristic of Balsas Basin Whiptail (*A. costatus costatus*), which may represent a local adaptation to high predation regimes on their eggs and/or to low survivorship rates (López-Moreno et al. 2016).

References

Barley AJ, Nieto-Montes de Oca A, Reeder TW, Manríquez-Morán NL, Arenas-Monroy JC, Hernández-Gallegos O, Thomson RC (2019) Complex patterns of hybridization and introgression across evolutionary timescales in Mexican whiptail lizards (*Aspidoscelis*). Molecular Phylogenetics and Evolution 132: 284–295. https://doi.org/10.1016/j.ympev.2018.12.016

Dearing MD, Schall JJ (1994) Atypical reproduction and sexual dimorphism of the tropical Bonaire Island whiptail lizard, *Cnemidophorus murinus*. Copeia 1994: 760–766. https://doi.org/10.2307/1447193

Dixon JR, Lieb CS, Ketchersid CA (1971) A new lizard of the genus *Cnemidophorus* (Teiidae) from Queretaro, Mexico. Herpetologica 27: 344–354. https://www.jstor.org/stable/3890849

Dunham AE, Miles DB (1985) Patterns of covariation in the life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. The American Naturalist 126: 231–257. https://doi.org/10.1086/284411

Fitch HS (1985) Variation in clutch and litter size in New World reptiles. University of Kansas Museum of Natural History Miscellaneous Publication 76: 1–76. https://doi.org/10.5962/bhl.title.16254

Goicoechea N, Frost DR, De la Riva I, Pelegrino KCM, Sites Jr J, Rodrigues MT, Padial JM (2016) Molecular systematics of teioid lizards (Teioidea/Gymnophthalmoidea: Squamata) based on the analysis of 48 loci under tree-alignment and similarity-alignment. Cladistics 32: 624–671. https://doi.org/10.1111/cla.12150

Gómez-Benitez A, López-Moreno AE, Walker JM, Vásquez-Alcántara E, Sánchez-Manjarrez D, Suárez-Rodríguez O, Hernández-Gallegos O (2016) *Aspidoscelis costata*. Scale variation. Mesoamerican Herpetology 3: 1089–1091.

Hernández-Gallegos O (2004) Demografía de los lacertilios del complejo *Aspidoscelis* (*Cnemidophorus*) *cozumela* (Sauria: Teiidae) y sus especies parentales, en la Península de Yucatán, México. Ph. D. Thesis Universidad Nacional Autónoma de México, México, 133 pp. http://132.248.9.195/ppt2004/0333085/Index.html

Hernández-Gallegos O, Domínguez-Vega H (2012) Cambio estacional en la coloración dorsal de la lagartija *Aspidoscelis costata costata* (Squamata: Teiidae). Revista de Biología Tropical 60: 405–412. https://doi.org/10.15517/rbt.v60i1.2775

Hernández-Gallegos O, Pérez-Almazán C, López-Moreno AE, Granados-González G, Walker JM (2011) *Aspidoscelis sacki* (Sack's Spotted Whiptail). Natural History Note. Herpetological Review 42: 428.

Hernández-Gallegos O, Rodríguez-Romero FJ, Sánchez-Nava P, Méndez FR (2009) Rediscovered population of Mexican plateau spotted whiptail lizard, *Aspidoscelis septemvittata* (Teiidae), from México, D. F. Western North American Naturalist 69: 49–55. https://doi.org/10.3398/064.069.0115

Horváthova T, Cooney CR, Fitze PS, Oksanen TA, Jelic D, Ghira I, Uller T, Jandzik D (2013) Length of activity season drives geographic variation in body size of a widely distributed lizard. Ecology and Evolution 3: 2424–2442. https://doi.org/10.1002/ece3.613

Huey RB, Pianka ER (1981) Ecological consequences of foraging mode. Ecology 62: 991–999. https://doi.org/10.2307/1936998

Lemos-Espinal J, Ballinger R, Smith G (1998) Comparative demography of the high-altitude lizard, *Sceloporus grammicus* (Phrynosomatidae), on the Iztaccihuatl Volcano, Puebla, México. The Great Basin Naturalist 58: 375–379. https://www.jstor.org/stable/41713075

López-Moreno AE, Rheubert JL, Pérez-Almazán C, Granados-González G, Hernández-Hernández LE, Gribbins KM, Hernández-Gallegos O (2016) Female reproductive cycle and clutch size of *Aspidoscelis costata costata* (Squamata: Teiidae) from Tonatico, Estado de México. Revista Mexicana de Biodiversidad 87: 1336–1341. https://doi.org/10.1016/j.rmb.2016.10.004

Manríquez-Morán NL, Villagrán-Santa Cruz M, Méndez-de la Cruz FR (2005) Reproductive biology of the parthenogenetic lizard, *Aspidoscelis cozumela*. Herpetologica 61: 435–439. https://doi.org/10.1655/04-41.1

Maslin TP, Secoy DM (1986) A Checklist of the Lizard Genus *Cnemidophorus* (Teiidae). Contributions in Zoology, University of Colorado Museum, 60 pp.

McCoy CJ, Hoddenbach GH (1966) Geographic variation in ovarian cycles and clutch size in *Cnemidophorus tigris* (Teiidae). Science 154: 1671–1672. https://doi.org/10.1126/science.154.3757.1671

Meiri S, Bauer AM, Chirio L, Colli GR, Das I, Doan TM, Feldman A, Castro Herrera F, Novosolov M, Pafilis P, Pincheira-Donoso D, Powney G, Torres-Carvajal O, Uetz P, Van Damme R (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. Global Ecology and Biogeography 22: 834–845. https://doi.org/10.1111/geb.12053

Meiri S (2018) Traits of lizards of the world: Variation around a successful evolutionary design. Global Ecology and Biogeography 27: 1168–1172. https://doi.org/10.1111/geb.12773

Méndez de la Cruz FR, Guillette LJ, Villagrán Santa Cruz M (1993) Differential atresia of ovarian follicles and its effect on the clutch size of two populations of the viviparous lizard *Sceloporus mucronatus*. Functional Ecology 7: 535–540. https://doi.org/10.2307/2390129

Méndez-de la Cruz FR, Díaz de la Vega-Pérez A, Centenero-Alcalá E, Jiménez-Arcos V (2018) Anfibios y Reptiles del Parque Nacional la Malinche, Universidad Autónoma de Tlaxcala, 137 pp.

Mesquita DO, Faria RG, Colli GR, Vitt LJ, Pianka ER (2016) Lizard life-history strategies. Austral Ecology 41: 1–5. https://doi.org/10.1111/aec.12276

Muñoz-Manzano JA (2010) Dieta de *Aspidoscelis costata costata* (Squamata: Teiidae) en el sur del Estado de México. Bachelor Thesis, Universidad Autónoma del Estado de México, México, 41 pp.

Novosolov M, Raia P, Meiri S (2013) The island syndrome in lizards. Global Ecology and Biogeography 22: 184–191. https://doi.org/10.1111/j.1466-8238.2012.00791.x

Paulissen MA (1987) Optimal foraging and intraspecific diet differences in the lizard *Cnemidophorus sexlineatus*. Oecologia 71: 439–446. https://doi.org/10.1007/BF00378719

Ramírez-Bautista A, Balderas-Valdivia C, Vitt LJ (2000) Reproductive ecology of the whiptail lizard *Cnemidophorus lineatissimus* (Squamata: Teiidae) in a tropical dry forest. Copeia 2000: 712–722. https://doi.org/10.1643/0045-8511(2000)000[0712:REOTWL]2.0.CO;2

Ramírez-Bautista A, Leyte-Manrique A, Marshall JC, Smith GR (2011) Effects of elevation on litter-size variation among lizard populations in the *Sceloporus grammicus* complex (Phrynosomatidae) in Mexico. Western North American Naturalist 71: 215–221. https://doi.org/10.3398/064.071.0208

Reeder TW, Cole CJ, Dessauer HC (2002) Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): A test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. American Museum Novitates 3365: 1–61. https://doi.org/10.1206/0003-0082(2002)365<0001:PROWLO>2.0.CO;2

Sales RFD, Ferire EMX (2016) Reproductive biology of a whiptail lizard (Teiidae: *Ameivula*) in the Brazilian Caatinga. Salamandra 52: 189–196.

Stearns SC (1989) Trade offs in life-history evolution. Functional Ecology 3: 259–268. https://doi.org/10.2307/2389364

Suárez-Rodríguez O, Suárez-Varón G, Chávez-Siles F, Pérez-Arriaga F, Andrade-Soto G, Aguilar-Isaac L, Sherbrooke WC, Hernández-Gallegos O (2018) Masa relativa de la camada en *Phrynosoma orbiculare* (Squamata: Phrynosomatidae) en el Parque Estatal Sierra Morelos, Toluca, Estado de México. Revista Mexicana de Biodiversidad 89: 282–289. https://doi.org/10.22201/ib.20078706e.2018.1.1925

Suárez-Varón G, Suárez-Rodríguez O, Granados-González G, Villagrán-Santa Cruz M, Gribbins KM, Cortez-Quezada D, Hernández-Gallegos O (2019) Relative clutch mass of *Basiliscus vittatus* Wiegmann, 1828 (Squamata, Corytophanidae): female morphological constraints. Herpetozoa 32: 211–219. https://doi.org/10.3897/herpetozoa.32.e35910

Taylor HL, Droll BA, Walker JM (2006) Proximate causes of a phylogenetic constraint on clutch size in parthenogenetic *Aspidoscelis neotesselata* (Squamata: Teiidae) and range expansion opportunities provided by hybridity. Journal of Herpetology 40: 294–304. https://doi.org/10.1670/0022-1511(2006)40[294:PCOAPC]2.0.CO;2

Taylor HL, Cooley CR, Aguilar RA, Obana CJ (1992) Factors affecting clutch size in the Teiid lizards *Cnemidophorus tigris gracilis* and *C. t. septentrionalis*. Journal of Herpetology 26: 443–447. https://doi.org/10.2307/1565121

Tinkle DW (1972) The dynamics of a Utah population of *Sceloporus undulatus*. Herpetologica 28: 351–359. https://www.jstor.org/stable/3890671

Tucker DB, Colli GR, Giugliano LG, Hedges SB, Hendry CR, Lemmon EM, Lemmon AR, Sites Jr JW, Pyron RA (2016) Methodological congruence in phylogenomic analyses with morphological support for teiid lizards (Sauria: Teiidae). Molecular Phylogenetics and Evolution 103: 75–84. https://doi.org/10.1016/j.ympev.2016.07.002

Uetz P, Freed P, Hošek J [Eds] (2020) The Reptile Database. http://www.reptile-database.org/

Ugueto GN, Harvey MB (2010) Southern Caribbean *Cnemidophorus* (Squamata: Teiidae): description of new species and taxonomic status of *C. murinus ruthveni* Burt. Herpetological Monographs 24: 111–148. https://doi.org/10.1655/HERPMONOGRAPHS-D-10-00002.1

Utsumi K, Kusaka C, Pedersen R, Staley C, Dunlap L, Smith SG, Eifler MA, Eifler DA (2020) Habitat-dependent search behavior in the Colorado Checkered Whiptail (*Aspidoscelis neotesselata*). Western North American Naturalist 80: 11–18. https://doi.org/10.3398/064.080.0102

Vitt LJ, Congdon JD (1978) Body shape, reproductive effort and relative clutch mass in lizards: resolution of a paradox. The American Naturalist 112: 595–608. https://doi.org/10.1086/283300

Vitt LJ, Pianka ER (2004) Historical patterns in lizard ecology: What teiids can tell us about lacertids. In: Pérez-Mellado V, Riera N, Perera A (Eds) The biology of lacertid lizards evolutionary and ecological perspectives, Institut Menorqui d' Estudis, Recerca, España, 139–157.

Vitt LJ, Price HJ (1982) Ecological and evolutionary determinants of relative clutch mass in lizards. Herpetologica 38: 237–255. https://www.jstor.org/stable/3892377

Vitt LJ, Breitenbach GL (1993) Life histories and reproductive tactics among lizards in the genus *Cnemidophorus* (Sauria: Teiidae). In: Wright JW, Vitt LJ (Eds) Biology of Whiptail Lizards (Genus *Cnemidophorus*). Oklahoma Museum of Natural History, Oklahoma, 211–244.

Walker JM (1981) Reproductive characteristics of sympatric whiptail lizards (Genus *Cnemidophorus*) in Southern México. Journal of Herpetology 15: 321–328. https://doi.org/10.2307/1563436

Walker JM (1982) Reproductive characteristics of the Colima Giant Whiptail, *Cnemidophorus communis communis* Cope. The Southwestern Naturalist 27: 241–243. https://doi.org/10.2307/3672908

Walker JM, Lemos-Espinal JA, Smith HM (2003) *Cnemidophorus costatus barrancarum* (Barranca Whiptail Lizard). Reproduction. Herpetological Review 34: 366–366.

Walker JM (2008a) *Aspidoscelis costata huico* (Blue-chested Whiptail). Reproduction. Herpetological Review 39: 85–86.

Walker JM (2008b) *Aspidoscelis costata nigrigularis* (Sinaloa Black-throated Whiptail). Reproduction. Herpetological Review 39: 86–87.

Walker JM (2010) *Aspidoscelis costata griseocephala* (Blue-throated Whiptail). Reproduction. Herpetological Review 41: 351–351.

Zanchi-Silva D, Borges-Nojosa DM, Galindo CA (2014) Reproduction of a whiptail lizard (*Ameivula ocellifera*, Teiidae) from a coastal area in northeastern Brazil. Anais da Academia Brasileira de Ciências 86: 1263–1272. https://doi.org/10.1590/0001-3765201420130153